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Climate, rather than human disturbance, is the main driver of age-specific mortality trajectories in a tropical tree

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ABSTRACT

Environmental and anthropogenic stressors can interact (e.g., drought, harvest or herbivory) to shape plant demography and evolutionary strategies with implications for sustainable resource management plans. Harvest or recurrent biomass removal can act as a selective force. However, our understanding of how harvest and changes in climate can synergistically shape plant evolutionary strategies is limited. We used age-from-stage matrix modeling to investigate how chronic anthropogenic disturbance (severe foliage and bark harvest) affects age-specific mortality trajectories of a tropical tree, *Khaya senegalensis* in two contrasting climatic regions (dry versus moist) in West Africa. We then developed a stochastic model to test if changes in disturbance regime and the environmental conditions in which a cohort is born may alter stochastic age-specific mortality rates. The effect of harvest on age-specific mortality trajectories was modest and only noticeable in the moist region. Age-specific mortality trajectories differed significantly between regions. In the moist region, mortality rates decreased with age for the first 30 years of life to a minimum rate and then increased gradually after to reach an old age mortality plateau. In the dry region, mortality rates decreased with age to reach a plateau asymptotically. This difference in age-specific mortality trajectory is due to a greater delay in reaching reproductive size/age in the dry region. Our findings underscore intraspecific variation in age-specific mortality schedules and indicate that climatic effect may override the impact of anthropogenic activities on plant demography. Harvest, by favoring fast life stage transition to reproductive stages, can buffer the effect of drought.

1. Introduction

Understanding the age patterns of mortality has long been of fundamental interest for evolutionary ecologists, because such patterns unveil selective forces and evolutionary history (Hamilton, 1966; Crews, 1993; Vaupel et al., 1998; Larson, 2001; Tuljapurkar et al., 2007). Evidence is accumulating that age-specific mortality trajectories are highly diverse across the tree of life (Jones et al., 2014; Horvitz and Tuljapurkar, 2008; Metcalf et al., 2009; Salguero-Gómez et al., 2013; Baudisch et al., 2013), ranging from trajectories with increasing to decreasing or constant mortality rates with age (Silvertown et al., 2001; Roach and Gampe, 2004; Horvitz and Tuljapurkar, 2008; Garcia et al., 2011; Baudisch et al., 2013). For stage-structured populations, these trajectories converge toward an asymptote, a late age mortality plateau, which represents the long-term age-specific mortality rate (Horvitz and Tuljapurkar, 2008). Our understanding of how global changes may alter species life history particularly intraspecific variation in age-specific mortality trajectories in plants, is limited (Salguero-Gómez et al., 2013). Existing studies mostly focus on vertebrate and bird species and show that individuals adapt to environmental conditions they experience throughout life by means of different age-specific mortality schedules (Lemaître et al., 2015). Given that global change projections indicate frequent and longer drought spells (Allen et al., 2010), knowledge about adaptive shaping of demographic patterns will be crucial to gain a mechanistic understanding of plant populations response to chronic anthropogenic disturbance under climate change scenarios.

A recent study examines how hunting – as a form of harvest – can

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alter the rate of senescence for lesser snow geese in the wild in Canada and suggests no significant effect (Koons et al., 2014). Obviously hunting, which is akin to logging trees, removes individual from the population. Therefore the effect of this kind of lethal harvest on age-specific mortality trajectories is rather direct and may not affect species aging patterns. Non-lethal harvest of plants is widespread in the wild and this may offer a better opportunity to examine the ways in which chronic human disturbance affects life history and changes tree senescence (Gaoue et al., 2013). Non-lethal harvesting of wild plants often involves removal of products such as fruits, foliage, bark and resin, known as non-timber forest products (NTFP) and which serve as important source of food, medicine and contribute to the livelihoods of millions of people worldwide (Ticktin, 2004; Birch et al., 2010). NTFP harvest does not always lead to direct death of harvested individuals; however it can have far reaching ecological and evolutionary impacts both at the population and community levels (Moegenburg and Levey, 2002; Trauernicht et al., 2006; Gaoue and Ticktin, 2010). Non-timber forest products harvest can reduce population growth rate in both constant (Schmidt et al., 2011) and stochastic environments (Ticktin et al., 2002) with significant changes to plant life history traits. For example, harvesting can alter plant leaf economics (Gaoue et al., 2011b) with further reduction of individual size and delay the onset of reproduction (McGraw, 2001; Law and Salick, 2005; Gaoue et al., 2013). The effects of non-lethal harvest on plant life history can further be exacerbated by drought. For example, greater cost of adaptation to drought often leads to slower individual growth rate in dry areas (Tyree and Ewers, 1991). This reduction in growth can potentially delay reproduction, and change the patterns of age-specific mortality from that of populations in moist environments with faster individual growth. In this study, we investigated how climate and non- lethal harvesting of wild plants for non-timber forest products affect age-specific mortality patterns.

Studies on the age-specific mortality of plants are rare (Roach et al., 2009; Roach, 2012). This is partly due to difficulties in estimating individual plant age. For relatively short-lived plants, it is possible to conduct experiments where multiple cohorts are planted and tracked over multiple years so as to describe the age-specific demography (see Roach, 2003; Roach and Gampe, 2004; Picó and Retana, 2008). However, for long-lived plants such as trees, such experiment may not be feasible over a long enough time period to cover that lifespan. Other alternatives include using molecular based techniques (Ally et al., 2010) or dendrochronology (von Arx et al., 2006) to estimate plant age and then determine age-specific mortality trajectories. Recent developments in matrix theory provide analytical tools to estimate age-specific demographic (mortality and reproductive) rates in both deterministic and stochastic environments using stage-structured projection matrices (Cochran and Ellner, 1992; Horvitz and Tuljapurkar, 2008; Caswell and Salguero-Gómez, 2013). This approach has already been used to study the dynamics of age-specific mortality in plants (e.g. Silvertown et al., 2001; Metcalf et al., 2009; Baudisch et al., 2013), and provides rare opportunities to investigate how species ranking in the fast-slow life history continuum predicts the rate of demographic senescence (Jones et al., 2008, 2014). Using the age-from-stage modeling ultimately furthers our understanding of the evolution of senescence across the tree of life (Shefferson et al., 2017), particularly the rarity of senescence in angiosperms and long-lived plants species which were previously less understood (Baudisch et al., 2013). However these studies either did not account for environmental stochasticity or consider among populations variation in age-specific mortality rate.

Here, we used four years of demographic data from twelve populations with different harvesting histories and age-from-stage matrix modeling to estimate age-specific mortality rate for *Khaya senegalensis* (Meliaceae) in two climatic regions of Benin, West Africa. *K. senegalensis* is a tropical tree harvested for its bark as medicine and its foliage as an important source of fodder for cattle during the dry season (Gaoue and Ticktin, 2007). Foliage and bark harvesting, in most cases, does not kill adult individuals but alter their growth and reproductive patterns (Gaoue et al., 2011a; Bufford and Gaoue, 2015). Because the NTFP harvest system we studied is particular and harvesting in this case is non-lethal, it is possible to model at the individual or population level, different temporal sequences of foliage and bark harvest. In previous studies, Gaoue et al. (2011a) and Gaoue et al. (2013) show that consistent with local harvesters' practices (see Gaoue and Ticktin, 2009; Turner et al., 2000), the stochastic sequence of harvest intensities matters. The intensity of foliage harvest by the Fulani harvesters in a given year depends on previous year harvesting intensity (Gaoue and Ticktin, 2009). In addition, a population harvested at high (**H**) intensity (e.g., > 90% of branches pruned) for five consecutive years and then at low (**L**) intensity (e.g., < 10% of branches pruned) for the next five years (**HHHHHLLLLL**) would respond differently from one that has experienced five years of high and five years of low harvest intensity but spread out over the 10 years time period (**HLHLHLHLHL**). Consistent with this, Tuljapurkar and Haridas (2006) show that temporal autocorrelation can have a sizable effect on population dynamics. The effect of any sequence of harvest on population demography will depend on the ecological conditions in which harvesting takes places.

In this study, we take advantage of a detailed demographic dataset on *K. senegalensis* in two contrasting climatic regions of Benin (West Africa) to test the effects of climatic differences between regions (dry vs. moist) and harvest strategies (constant vs. stochastically variable rate) on its age-specific risk of mortality. We modeled the stochastic temporal sequence of harvest using a Markov process which allows us to test the effect of varying harvest intensity for a given site. By using a Markov process to model the temporal sequence of Fulani harvesting practices, we assumed that harvesting is not done randomly but that there is a temporal autocorrelation in harvesting intensities over time (Caswell, 2001; Gaoue et al., 2011a; Tuljapurkar et al., 2003). Our study indicates that difference in climate drives the dynamics of the age-specific mortality trajectories, whereas the impact of harvesting, regardless of the strategy, on these trajectories is modest.

2. Materials and methods

2.1. Study system

African mahogany, *K. senegalensis* (Meliaceae), is a tropical tree distributed in Africa across multiple habitats, from gallery forests to savanna woodland between 8° and 14° N (Normand and Sallenave, 1958; CTFT, 1988). The tree is a semi-deciduous, shade intolerant monoecious tree with wind-dispersed flat winged seeds, and insect-pollinated small white hermaphrodite flowers (CTFT, 1988). *K. senegalensis* is a slow growing tree that may reach up to 30 m in height. In Benin, it reaches an observed maximum diameter at breast height (dbh) of 136.2 cm (Gaoue and Ticktin, 2007; Gaoue et al., 2014) which would be the equivalent of 187 years considering an average diameter increment of 0.73 cm/yr for most tree species in the region (see Sokpon and Biaou, 2002). We studied the dynamics of *K. senegalensis* populations in two contrasting ecological regions in Benin, West Africa. These two regions cover the latitudes (8°–12° N) at which the species is found in its distribution range in Africa. The Sudanian region (9°30–12° N) is dry with lower rainfall (800–1000 mm/year), fewer rainy months, shorter plant growing season (145 days), and higher mean temperature (2431 °C) than the moist Sudano-Guinean region (7°30–9°30 N; annual rainfall: 1000–1300 mm/year, plant growing period: 200 days, temperature: 25–29 °C). Details about the ecological differences between the dry and moist regions are provided elsewhere (Gaoue and Ticktin, 2007, 2010).

K. senegalensis was one of the first timber species exported from Africa during the colonial era (Normand and Sallenave, 1958). Commercial companies and local populations illegally harvested the timber to depletion in several part of its distribution range. Foliage is heavily harvested from remnant standing populations by indigenous Fulani

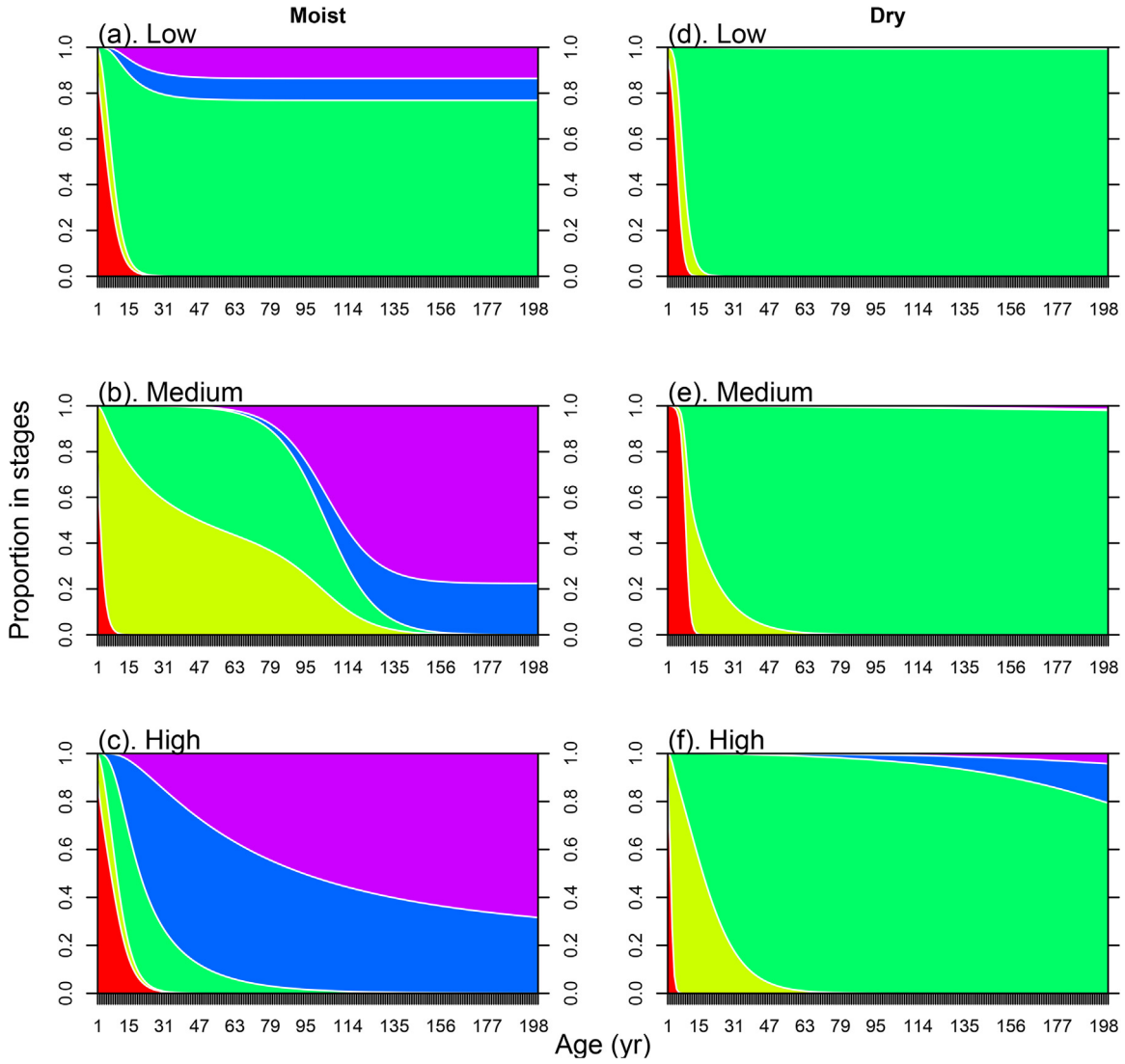

Fig. 1. The age-specific stage structures varied between regions and harvest levels. Each color represents a unique life stage: seedling (red), sapling (yellow), juvenile (green), small adult (blue), large adult (purple). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

people across West Africa to feed cattle during the peak dry season (Petit, 2003; Gaoue and Ticktin, 2007). The Fulani specialize in raising cattle, which are a vital source of income for them and an integral part of their culture (Gaoue and Ticktin, 2009). Harvested *K. senegalensis* trees often lose > 80% of their canopy (Gaoue and Ticktin, 2007) and most of harvested populations have been pruned since the severe drought of the 1970s (L'hote et al., 2002).

2.2. Demographic data

We collected data on growth, survival and fruit production of *K. senegalensis* individuals over 4 years (2004 − 2007), in twelve 1-ha permanent plots equally distributed between the dry and moist regions. *K. senegalensis* only occurs in gallery forest in the dry region whereas in the moist region it is also found in dry dense forest and woodland. We established our study populations to sample across the range of these differences in habitat and harvest intensity. For each population, we estimated the percent of trees harvested (pruned and/or debarked). Individuals trees were more likely pruned than debarked and we assumed the former would have stronger effects on population demography. Pruned trees often have > 80% of their canopy harvested while at most < 25% of trunk were debarked (Gaoue and Ticktin, 2007). Using this harvesting data and following Gaoue et al. (2011a, 2013), we categorized each population into one of three levels of harvest intensity (low, medium, or high) depending on the proportion of trees harvested for foliage and bark. Populations with fewer than 25% of trees harvested were classified as low harvest (**L**); medium harvest (**M**) populations were those with 25–50% of trees harvested and high harvest (**H**) populations had more than 50% of trees harvested. In the moist region, we were able to find and survey three low, two medium and one high harvest populations; while in the dry region, there were three low, one medium and two high harvest populations. Our study, with 12 independent populations, represents one of the largest sample sizes in demographic studies (Salguero-Gómez et al., 2015). However, such unbalanced design limited our ability to uncover any non-linear response to harvest but still allowed to test for the global effect of harvest on age-specific mortality.

2.3. Age-from-stage matrix model

For each population and year we built a 5 × 5 stage-based projection matrix **A** (Caswell, 2001). We defined five life stages using the basal diameter for seedlings and saplings, and diameter at breast height (dbh) for juvenile and adults, based on previous results on the size

specific survival and reproduction (see Gaoue and Ticktin, 2008, 2010, for details): seedlings (basal diameter < 2 cm), saplings (2–5 cm), juveniles (5–20 cm), small reproductive (20–40 cm), and large reproductive adults (dbh ≥ 40 cm). Each matrix transition element was estimated only when we had more than 5 observations. For transition elements for which we have less than 5 individuals, we used values estimated from a pooled matrix across populations with similar climate and harvesting treatments. We averaged the elements of the projection matrices across populations and years by harvest intensity to obtain three matrices (low, medium and high) in each region. We split each matrix **A**, into a fertility matrix **F** and a transition matrix **Q**, the latter representing only transitions among stages of already existing individuals: $\mathbf{A} = \mathbf{Q} + \mathbf{F}$. The stage duration matrix **N**, also known as the fundamental matrix, which captures how much time an individual plant is expected to spend in each life stage before dying (Cochran and Ellner, 1992):

$$\mathbf{N} = (\mathbf{I} - \mathbf{Q})^{-1}, \quad (1)$$

where **I** is an 5 × 5 identity matrix. We estimated mean survivorship to age x for populations harvested at constant rate over time following Caswell (2001):

$$l(x) = e^T \mathbf{Q}^x, \quad (2)$$

where e^T is a 5 × 1 column vector of ones used to sum up the columns of matrix $\mathbf{Q}^x$. By varying the age x, we established the age-specific stage structure which captures the variation in the proportion of each *K. senegalensis* life stages over time (see Fig. 1). We performed the above analysis for each of the six **Q** matrices (two climatic regions × three harvest intensities). We calculated the age-specific mortality rate $\mu(x)$, the rate of decrease in survivorship, as follows (Horvitz and Tuljapurkar, 2008):

$$\mu(x) = \log l(x) - \log l(x+1), \quad (3)$$

where $l(x+1)$ is the survivorship to age $x+1$. The age-specific mortality trajectory may show different patterns of increasing or decreasing rates with age, but eventually will converge to an asymptote, $-\log\lambda$, where λ is the dominant eigenvalue of matrix **Q**. This asymptote is the mortality plateau and represents the long-term rate of mortality (Horvitz and Tuljapurkar, 2008).

2.4. Simulating stochastic harvest environments

Calculating the mean survivorship to age x when harvest intensity varies stochastically over time requires a Markov chain model for the harvest dynamics, essentially a model of environmental dynamics, where each state of the environment corresponds to one of three harvest intensities: low, medium and high (see for details Gaoue et al., 2011a, 2013). We modeled the temporal sequence of harvest intensity as a stochastic Markov process using 3 × 3 Markov transition matrices **C** that define probability rules to generate a temporal sequence of harvest intensities that a given population will experience over the long run (Tuljapurkar et al., 2003; Gaoue et al., 2013). Each matrix element $c_{\alpha\beta}$ represents the probability that a population that is currently harvested at intensity β will be harvested at intensity α the next year. To generate plausible temporal sequences of harvesting pressures for a given population, we created 36 different 3-state Markov chains, **C**. These chains were selected to each simulate a specific management option and to represent a range of harvesting pressure which was measured by their return times to high harvest.

Each Markov chain, **C**, can be characterized by its serial autocorrelation and a return time to high harvest, which is the average number of years spent in each state of the environment before returning to a high harvest year. To calculate the return time to high harvest for each Markov chain model of harvest dynamics, we use the environment-level analogue to the fundamental matrix **N** in Eq. (1) (see Caswell, 2001; Tuljapurkar and Horvitz, 2006, for detailed method). In this environmental state duration equation, we considered high harvest intensity state, **H**, as the absorbing state (or death); that is to replace all the elements of the third row (which represents high harvest state) of Markov matrix **C** with zeros. Then, we determined the first passage time to the absorbing state **H** for populations starting at a high harvest intensity, using the sum of the column **H** (for high level of harvest intensity) of the fundamental matrix of the modified Markov chain. The return times for the 36 Markov chains ranged from 1.11 to 99.11 years. Smaller return times represent high harvesting pressure (high frequency of high harvest years) and larger values represent low pressure (low frequency of high harvest years) (see Gaoue et al., 2013).

2.5. Age-specific mortality in stochastic environments

We then construct a model that includes environmental dynamics and life-stage transitions in each state of the environment to determine the mean survivorship to age x of a cohort in the context of a dynamic harvesting environment. Since all individuals are born into one specific harvest environment or another, specified as a, we calculated $l_a(x)$, the average survivorship to age x for all individuals born in harvest environment a. Here, $l_a(x)$ is calculated for each of the 3 harvest intensities, a, as the sum of the first column of the matrix on the right side of the following equation (Tuljapurkar and Horvitz, 2006; Metcalf et al., 2009):

$$l_a(x) = [\tilde{e}\mathbf{m}^{x-1}\tilde{\mathbf{Q}}_a]_1, \quad (4)$$

where the subscript 1 indicates the first column of the matrix, $\tilde{e}$ is a block matrix made up of a row of 3 blocks where each block is **I**, $\tilde{\mathbf{Q}}_a$ is a block matrix made up of a column of 3 blocks, where each block is an 5 × 5 matrix and only the ath block is nonzero and its corresponding **Q** matrix; and **m** is the 15 × 15 megamatrix that combines the population and environment level dynamics (Pascarella and Horvitz, 1998; Tuljapurkar and Horvitz, 2006):

$$\mathbf{m} = (\mathbf{C} \otimes \mathbf{I})\mathbf{U}_a, \quad (5)$$

where $\mathbf{U}_a$ is also a block matrix of 3 × 3 blocks, each 5 × 5 with zeros everywhere except in the blocks that form the diagonal of the block matrix where the three **Q** are inserted, ⊗ is the Kronecker product, and **C** is a 3 − state harvest Markov transition matrix as described above. We provide R scripts to estimate the age-specific survivorship and mortality risk both in constant and stochastic environments at https://github.com/ogaoue/age-from-stage. The population mean matrices and Markov chains used for these analyses are available in Dryad Digital Data Repository (Gaoue et al., 2013; Gaoue, 2015, 2016).

3. Results

3.1. Age-specific population structure

Cohorts of *K. senegalensis* born in different environments differ markedly in the stages they were projected to attain by certain ages, especially between dry and moist regions. In the dry region, most individuals remain in the juvenile stage even though they may attain 186 years of age (Fig. 1 d, e), indicating a delay in reaching maturity. Nearly 100% of the old individuals in the low and medium harvest environments are juveniles, while in the high harvest environment, 20% of the survivors will be in the adult phase by this age (Fig. 1 f). In contrast, in the moist region, plants mature more rapidly than in the dry region. By 186 years of age, 20%, 100% and 100% of survivors are reproductive adults respectively in the low, medium and high harvest environments (Fig. 1 a − c). Surprisingly, the proportion of a cohort that attains reproductive status by late ages is lowest in the low harvest environments in both moist and dry regions (Fig. 1 a, d compared to the others). All together, harvest facilitated the transition to reproductive stages regardless of the environmental conditions. However, this process was the fastest in more challenging environmental conditions.

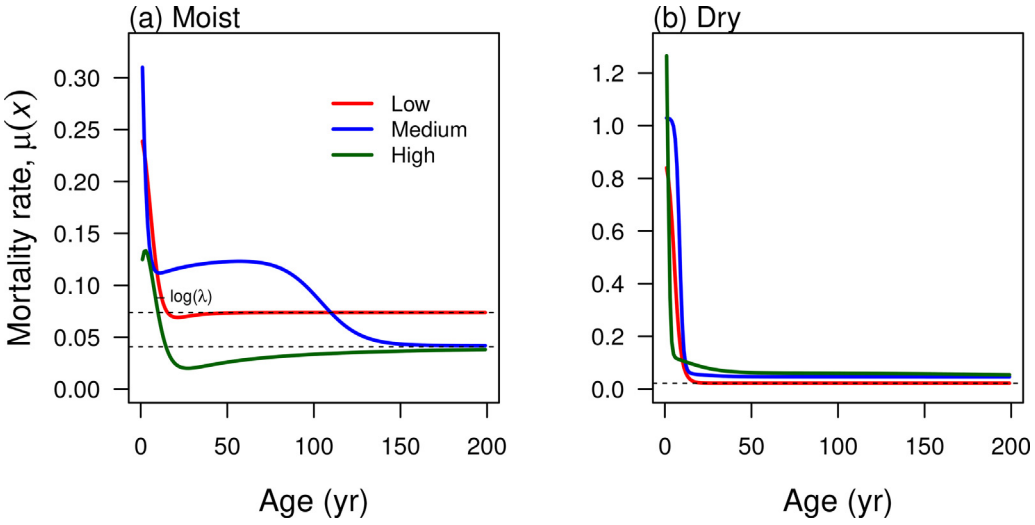

Fig. 2. Age-specific (a, b) mortality trajectories in constant environments for moist and dry regions. Each line represents population harvest intensity (low or high), and the dotted lines at $-\log\lambda$ represent the mortality plateau.

3.2. Effects of harvest and climate on age-specific mortality in constant environments

For populations harvested at constant rate over time, patterns of age-specific mortality rate varied between regions. Mortality trajectories plateaued at different ages, depending upon harvesting intensity (Fig. 2 a, b). In both regions, the rate of mortality was higher at young ages, and quickly declined within the first 20 years, quicker in the dry region than in the moist. In the moist region, mortality trajectories in the low and high harvest populations showed a bathtub shape, and plateaued from the bottom (Fig. 2 a). Young individuals escaped juvenile mortality after about 20 years and risk of mortality gradually increased thereafter to reach a mortality plateau, the long-term rate of mortality. Individuals in low harvest populations escaped juvenile mortality (after 10 years) and their mortality trajectory plateaued (at around 35 years) the fastest but had a higher long-term mortality rate than those in high harvest populations. The mortality plateau was the same for high and medium harvest populations.

In the dry region, age-specific mortality rates declined quickly and plateaued from the top (Fig. 2 b). Similar to the moist region, the plateau was reached first in low harvest populations (after 20 years), then in the medium harvest populations (after 30 years) and later by high harvest populations after 50 years. However, contrary to the moist region, the mortality plateau for low harvest populations was lower than the one in medium or high harvest populations.

3.3. Age-specific mortality in stochastic environments

For models with variable harvesting intensity over time, age-specific mortality trajectories showed more variance between harvest sequences in the moist (Fig. 3 a) than in the dry region (Fig. 3 b). In the dry region, for each harvesting sequence, mortality rate dropped gradually to reach a plateau (Fig. 3 b). The values of the mortality plateau were lower when harvesting pressure was high than when harvesting pressure decreased (Fig. 3 c). This suggests that the mortality plateau was reached earlier for populations under high harvest pressure than the ones that were allowed more time to recover. In the moist region, except for a few harvesting sequences, mortality trajectories departed from the general trend found in dry region (Fig. 3 a).

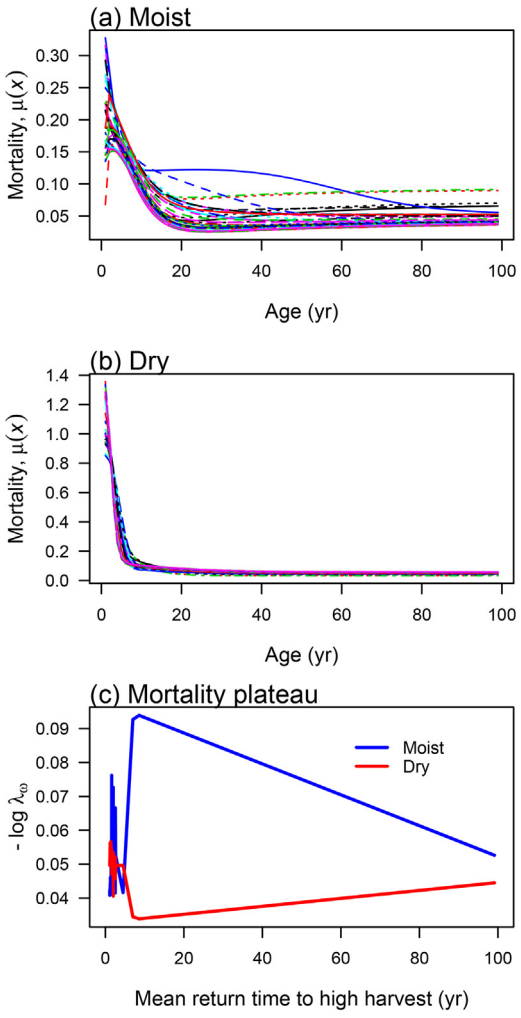

Fig. 3. Age-specific stochastic mortality trajectories for 36 sequences of harvest with mean return time to high harvest ranging from 1.1 to 99 years, in (a) moist versus (b) dry regions. Each line represents a specific sequence. (c) The stochastic mortality rates, $-\log\lambda_{\omega}$, followed a different pattern between the two regions for mean return time greater than 8 years. These trajectories did not differ between different initial environments and we present here the case for low harvest environments.

4. Discussion

We studied the effects of climatic differences, tree defoliation and

bark removal by indigenous people on the dynamics of population structure and age-specific mortality of African mahogany. Our results show a strong effect of climatic differences on the shape of age-specific mortality trajectories and long-term risk of mortality of *K. senegalensis*, as it is often the case for many overstory tree species (Nepstad et al., 2007; Phillips et al., 2010). These differences were driven by the effect of climatic difference on the dynamics of age-specific population structure (Fig. 1). Specifically, individual residence time in juvenile life stage (delay to reproduce) drives the shape of the mortality trajectories. In the dry region, as a response to drought, individuals reach reproductive size/age later than in the moist region (Gaoue and Ticktin, 2008). This delay in reaching reproductive size/age leads to juvenile-dominated cohorts over the long-term. In contrast, in the moist region, where individual growth is relatively fast, most individuals transition to the reproductive stage within 90 years (Fig. 1 b, c), with the exception of low harvest populations where juveniles dominate the population. Consequently, populations that experienced low harvest intensity in the moist region exhibit age-specific mortality trajectories (Fig. 2 a) that are similar to those observed in the dry region (Fig. 2 b). Our results illustrate that the extent of reproductive delay is critical in understanding the dynamics of age-specific mortality. The slight increase in mortality rate observed in the moist region when cohorts are dominated by newly reproductive trees may be due to the cost of accelerated juvenile growth (see Mangel and Munch, 2005).

We found greater differences in age-specific mortality trajectories between climatic regions than between harvesting intensities, suggesting that climate has a stronger effect on age- specific mortality than harvest. As a result of delayed reproduction and subsequent over-dominance of juveniles in the population structure over time in the dry region, the mortality trajectories approached the plateau from high values while the contrary was true for the moist region. Previous studies of *K. senegalensis* reported similar trends of a stronger effect of climate than non-timber forest products harvest on population dynamics (Gaoue and Ticktin, 2010; Gaoue et al., 2011a). These results are also consistent with recent reports on the significant role of climate rather than disturbance (but see Morrison et al., 2016) on forest composition (Rugemalila et al., 2016), diversity (Rito et al., 2017) and dynamics (Martinez Ramos et al., 2009; McEachern et al., 2009; Toledo et al., 2011). By comparing the two regions, our results provide insights into how plants may respond to change in climate. There is a gradual shift in climatic conditions in our study areas; the current dry region is projected to become drier and future climates in the moist region are likely to resemble those in the current dry region (Paeth and Hense, 2004). Under a drier climate scenario the age-specific mortality trajectories of *K. senegalensis* in the moist region will converge to the one currently observed in the dry region (Fig. 2 b). Reproductive stages might become critically rare in most populations of the study species under increased drought in all the regions. As demonstrated in our study (see Fig. 1), harvest by favoring transition to reproductive stages both in the moist and dry regions might buffer the effect of drought. Previous studies indicated that NTFP harvest has negative effects on both the short (Gaoue, 2016) and long-term (Gaoue et al., 2011a) dynamics of our study species, and other tropical plant species (Ghimire et al., 2008). Here we show that by investigating a different set of demographic parameters, beyond population growth rate, the effect of harvest may be beneficial (see also Fuller et al., 2015; Thom et al., 2017). However, it is simplistic to assume that this finding alone is evidence that harvesting must be encouraged as a strategy to limit the effect of climate change. A more global analysis of how harvest affects a wide range of demographic parameters (population growth rate, age at first reproduction, mortality trajectories, damping ratio), the yield and quality of harvested products is necessary to fully address this question (Gaoue et al., 2013).

A bathtub-like age-specific mortality trajectory is most commonly reported for iteroparous perennial plants (Silvertown et al., 2001). However, there is increasing evidence that a reduced mortality rate at older ages, is more common than previously thought (Vaupel et al., 2004) including in several tropical trees such as *Garcinia lucida* (Guedje et al., 2003) and *Cecropia obtusifolia* (Alvarez Buylla and Martinez-Ramos, 1992). Several other studies provided empirical evidence of a diversity of age-specific mortality trajectories in tropical and temperate trees (Silvertown et al., 2001; Horvitz and Tuljapurkar, 2008; Metcalf et al., 2009; Baudisch et al., 2013). Our results contribute to that body of work and indicate a climate-driven within-species variation in age-specific mortality trajectories. We demonstrate that, at least for our study species, such within-species variation is related to the extent of delay in reproduction across populations. One reason why most studies failed to elucidate the within species variation in mortality trajectories owe to the lack of spatial replication of study sites. A limited number of sites are often studied within the same ecological region where species have similar dynamics of age-specific mortality rate across sites. One of the strengths of our study is that we took advantage of large demographic dataset covering a total of twelve independent populations. This allowed us to examine the within species heterogeneity in mortality trajectories. In fact, by investigating how these trajectories change as a result of climatic difference and disturbance regimes that are frequent in our study region, NTFP harvest, we were able to show how harvest and climate related delay in reaching maturity size/age (see also Souther and McGraw, 2014), may lead to a diversity of mortality trajectories for a given species. Our results underscore the importance of long-term studies and of spatially heterogeneous data to further our understanding of population responses to disturbance, climate change and their interactions.

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